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Dynamics of Bimanual Rhythmic Coordination in the Coronal Plane

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We investigated the 1:1 frequency locking of two hand-held pendulums oscillated parallel to the body's coronal plane. In this configuration, anti-phase defined muscularly is in-phase defined spatially, and vice versa. Coordination equilibria measured by average relative phase were shifted less from muscular anti-phase than from muscular in-phase by detuning (unequal uncoupled pendulum frequencies) and were shifted less in both modes with vision than without. Variability of the equilibria, however, was ordered opposite to their degrees of shift and was unaffected by vision. Demonstrated subcritical pitchfork and tangent bifurcations conformed to the variability classification of anti- and in-phase coordination. Implications for dynamical models, hierarchical control, and definitions of coordination modes were discussed.

In Bernstein's (1996) hierarchical characterization of biological movement systems, the formation and selection of cooperative relations among relatively independent muscles spanning one or more joints are tasks of the level of muscular–articular links or synergies. According to Bernstein, the functioning of this level is oriented strictly to the patterning of the body's segments. The criteria that the level of synergies satisfies are with respect to the patterns themselves, namely, criteria of pattern stability and pattern retention (against both internal and external perturbations). Criteria having to do with the particular uses of the patterns in everyday activity are not the concern of the level of synergies. Satisfying criteria of the latter kind is the concern of other levels, specifically, the level of space and the level of actions. Under Bernstein's (1996) interpretation, the motor problems solved by the level of space are generically those of translating from an object's spatial coordinates to a sequence of muscle activation. Typical of the level of space are aimed, transferring movements, characterized by criteria of accuracy and precision. The class of motor problems solved by the level of actions is that of sequencing different movements that succeed each other systematically, leading to the solution of a problem whose meaning (function, purpose) dictates the relation among the components. Where corrections and adjustments at the level of synergies are based strictly on muscular proprioception, at the level of space they are based (primarily)

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on visual exteroception, proprioception, and exproprioception (see Lee, 1978), and at the level of actions they are based on plans and intentions.

In the present research we consider the relation between the levels of space and synergies by examining the influences of vision and of task orientation with respect to the principal body axes on an elementary rhythmic synergy: the 1:1 frequency locking of two contralateral segments of the body. One typical experimental procedure for studying this synergy requires oscillating two hand-held pendulums about the left and right wrist joints and parallel to the body's sagittal plane (e.g., Kugler & Turvey, 1987; Rosenblum & Turvey, 1988; Schmidt, Shaw, & Turvey, 1993; Sternad, Turvey, & Schmidt, 1992). The experimental advantage of using pendulums is control over the frequency competition between the left and right hands (see below). In the present research we used a variant of this typical procedure, where the hand-held pendulums were oscillated in a frontoparallel plane (parallel to the body's coronal plane) as shown in Figure 1. The significant feature of this particular 1:1 frequency locking task is that the in-phase (anti-phase) coordination from the perspective of the level of muscular–articular links or synergies is the anti-phase (in-phase) coordination from the perspective of the level of space (interpreted here as the visual perception of the ongoing coordination). When homologous muscles of the right and left forearms contract simultaneously, the pendulums move spatially in opposite directions.

The relation between Bernstein's level of synergies and level of space can be approached through the dynamical theory of coordination patterns developed by Schöner and Kelso (1988a, 1988b, 1988c, 1988d). The significance of this theory is that it aims to incorporate within a single formulation the fundamental dynamics of a particular coordination, called intrinsic dynamics, and the modulation of those dynamics by environmental and informational factors, called required dynamics. Rhythmically moving together two segments of the body in 1:1 frequency locking, as depicted in Figure 1, is an elementary coordination pattern. This pattern is a functional coordination in which many physical, biological, and psychological components relate in an ordered fashion. At the core of the dynamical theory of

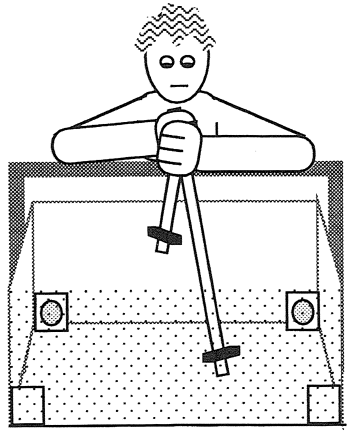

Figure 1 — Schematic of participant performing 1:1 frequency locking of hand-held pendulums oscillating parallel to the body's coronal plane.

coordination patterns are three propositions (see Schöner & Kelso, 1988a). First, on any level of analysis (kinematic, muscular, neural, and below), a coordination pattern is characterized by a low-dimensional collective variable or order parameter. Second, reproducible and stationary states of the coordination are mapped onto the attractors of the dynamics of this order parameter. Third, there are certain parameters (often one, sometimes a few) that act on the collective dynamics nonspecifically or indirectly, meaning, essentially, that there is no formal resemblance between these parameters and the resultant stationary states. Such parameters are called control parameters. These three propositions are at work in the formulation of the dynamical model of 1:1 frequency locking advanced by Haken, Kelso, and Bunz (1985), Schöner, Haken, and Kelso (1986), and Kelso, DelColle, and Schöner (1990) and are constrained by the empirical fact that anti-phase is less attractive than in-phase (e.g., Kelso, 1984):

$$\dot{\phi} = \delta - a \sin \phi - 2b \sin 2\phi + \sqrt{Q}\zeta_t \tag{1}$$

In Equation 1, the relative phase $\phi = \theta_{left} - \theta_{right}$ between the phase angles (θ_i) of the oscillating body segments is the collective variable or order parameter with the overdot on the left-hand side signifying its time derivative. The control parameter is the ratio, *b/a*, of the coefficients on the 2π periodic terms, which determines the relative strengths of the attractors at 0 and π phase relations when $\delta = 0$ and the relative strengths of the attractors in the vicinity of 0 and π when $\delta \neq 0$. The dynamics are symmetrical, that is, $\phi = -\phi$, when $\delta = 0$, and they are asymmetrical, that is, $\phi \neq -\phi$, when $\delta \neq 0$. The quantity δ represents the detuning or imperfection parameter (Strogatz, 1994) and is commonly represented by the difference in the uncoupled frequencies of the contralateral segments, $\omega_{left} - \omega_{right}$ (but see Collins, Sternad, & Turvey, in press; Sternad, Collins, & Turvey, 1995). The final term in Equation 1 represents a stochastic force of strength Q that arises from the very many subsystems that contribute to the behavior of the collective variable at time scales much faster than that of the collective variable. The presence of the final term means that the collective variable will fluctuate about its stationary value.

Predictions about the equilibria of the 1:1 coordination pattern and their relative stabilities follow by setting the left-hand side of Equation 1 equal to zero, ignoring the noise term, and solving for ϕ given specific values of δ and *b/a*. The stability measure is the slope at the zero crossing of the time-derivative of ϕ as a function of ϕ. Designating this slope by λ, $\lambda < 0$ signifies a stable equilibrium and $\lambda > 0$ signifies an unstable equilibrium. It can be shown (see Gilmore, 1981; Schöner et al., 1986) that the standard deviation of ϕ, that is, SDϕ, is given by

$$\mathrm{SD}\phi = \sqrt{\frac{Q}{2|\lambda|}} \tag{2}$$

For a fixed magnitude of Q, SDϕ grows as the inverse of $|\lambda|$. A large body of experimental evidence has confirmed the predictions that follow from Equations 1 and 2) (see summaries by Kelso, 1994; Schmidt & Turvey, 1995).

With respect to the experimental task depicted in Figure 1, Equation 1 can be taken as defining the dynamics at the level of synergies. These are the dynamics in which vision does not participate (the subject's eyes are closed or the oscillating hand-held pendulums are occluded) and only the haptic perceptual system contributes to the coordination. What might we expect when the experimental task is

performed with the benefit of vision? Consider the symmetrical case when the two hand-held pendulums are identical, that is, $\delta = 0$. A hypothesis of visual dominance assumes Equation 1 as the coordination dynamics but with the equilibria of $\phi = 0$ and $\phi = \pi$ defined visually. According to this hypothesis, if a subject performed the task with eyes open as compared to eyes closed, the stability ranking of the two equilibria would reverse. In short, vision dominates the dynamics at the level of synergies, such that the muscular–articular linkages are completely governed by visual criteria (e.g., Gibson & Radner, 1937). Using the definition of ϕ in muscular terms as the standard (coactivation of homologous muscles defines in-phase, $\phi = 0$, and coactivation of nonhomologous muscles defines anti-phase, $\phi = \pi$), then with eyes open the stability ranking would be $\pi > 0$ (i.e., anti-phase more stable than in-phase), whereas with eyes closed the stability ranking would be $0 > \pi$ (i.e., in-phase more stable than anti-phase), following the observation behind Equation 1. Numerical solutions of Equation 1 reveal that λ is greater for $\phi = 0$ than $\phi = \pi$, meaning smaller SDϕ (see Equation 2) at $\phi = 0$. When vision dominates, $\phi = 0$ in muscular coordinates becomes $\phi = \pi$ in visual–spatial coordinates. So in the presence of vision, SDϕ is larger, not smaller, for $\phi = 0$ in muscular coordinates than $\phi = \pi$ in muscular coordinates.

A second and more plausible hypothesis—one that is consistent with Bernstein's interpretation of the responsibilities of the levels of space and synergies—assumes that vision modulates rather than dominates. When a subject watches the two oscillating hand-held pendulums in the configuration of Figure 1 executing, say, $\phi = \pi$ in muscular coordinates, the deviation of ϕ from visually defined 0 defines a "force" (e.g., Schöner & Kelso, 1988) of magnitude proportional to the deviation. In the dynamical theory of coordination patterns, a "force" reflecting the superimposition of a required pattern on an intrinsic pattern is represented by an additional 2π periodic term in the order parameter equation (Schöner & Kelso, 1988a, 1988b, 1988c; Sim, Shaw, & Turvey, in press). Let Γ stand for relative phase in visual–spatial coordinates, so that when $\phi = 0$ and $\phi = \pi$ in muscular coordinates, Γ is made equal to π and Γ is made equal to 0, respectively. Equation 1 can then be amended as follows to include the influence of vision:

$$\dot{\phi} = \delta - a \sin \phi - 2b \sin 2\phi - c \sin(\Gamma - \phi) + \sqrt{Q}\zeta_t \qquad (3)$$

Equation 3 with the noise term excluded can be solved numerically for an intended coordination of muscular in-phase (in which case $\Gamma = \pi$) and for an intended coordination of muscular anti-phase (in which case $\Gamma = 0$)[1]. With $\delta = 0$, and with a and b assuming standard values (e.g., $a = b = 1$, see Schöner et al., 1986; Sternad, Amazeen, & Turvey, in press), and c set at a comparable value (e.g., $c = 2$), Equation 3 has equilibria at $\phi = 0$ and $\phi = \pi$ with SDϕ smaller at 0 than at π.

[1]The choice of the ordering of Γ and ϕ in the argument of the third sine function was dictated by the assumption that seeing the two hands in spatial in-phase (anti-phase) should aid moving the hands in muscular anti-phase (in-phase). Exploration of Equation 3 using the two forms of the argument, namely, $\Gamma - \phi$ and $\phi - \Gamma$, revealed that $\Gamma - \phi$ gave the intuited facilitation with $\phi - \Gamma$ having the opposite effect. We pursued Equation 3 as shown with the idea that if the results turned out counter to intuition, that is, that seeing spatial in-phase (anti-phase) hindered moving the hands in muscular anti-phase (in-phase), then due consideration would be given to the $\phi - \Gamma$ form of the argument.

When Equation 3 is compared with Equation 1—the comparison of 1:1 frequency locking with visual guidance and without visual guidance—the equilibria of Equation 3 are more stable than the equilibria of Equation 1. That is, when $\delta = 0$, vision does not affect the location of the attractors (equilibrium points) of the elementary rhythmic synergy but it does affect their strength. SDϕ should be lower in the presence of vision than in its absence.

Experiment 1

Experiment 1 was directed at the predictions of the visual dominance and the visual modulation hypotheses for $\delta = 0$. Subjects produced 1:1 frequency locking, in-phase and anti-phase, in the manner depicted in Figure 1 with identical pendulums in the left and right hands. They did so with eyes open (watching the pendular motions) and with eyes closed. Under both hypotheses, the fixed points of the coordination dynamics for both eyes open and closed should be at $\phi = 0$ and $\phi = \pi$. The two hypotheses differ with respect to predictions about degree of stability. According to the visual dominance hypothesis, SDϕ should be larger at $\phi = \pi$ in the absence of vision and larger at $\phi = 0$ in the presence of vision. According to the visual modulation hypothesis (Equation 3), SDϕ should be larger at $\phi = \pi$ in both the absence and presence of vision but it should be less at both equilibria in the presence of vision.

Method

Participants. Six men and 3 women, all graduate students at the University of Connecticut, volunteered to participate in the experiment. All 9 had participated in previous experiments on interlimb coordination using the hand-held pendulums procedure.

Design and Procedure. The data collected in this study were the movement trajectories of the two hand-held pendulums. Measures included the frequency of oscillation averaged over the two pendulums, ω_{ave}; the relative phase averaged across the trial (the estimate of the stable fixed point), ϕ_{ave}; and the standard deviation of relative phase (the estimate of fluctuations about the stable fixed point), SDϕ. Participants were instructed to maintain a muscular phase relation ψ of either $\psi = 0$ or $\psi = \pi$ either with or without visual information. In the visual condition, they visually monitored the movement of the bottom tips of the pendulums. In the nonvisual condition, the hand-held pendulums were occluded. The same symmetrical pair of pendulums ($\delta = 0$) was used throughout the experiment. Therefore, participants were tested under four conditions (2 ψ × 2 Vision Conditions), with three trials per condition. Order of conditions was completely randomized.

Apparatus and Data Collection. The hand-held pendulums were aluminum rods (1.2 cm diameter) with wooden handles (2.5 cm in diameter), each held in the center of the hand so that the pendulum was vertical and the hand was positioned at the center of the 12 cm long wooden handle attached at the top. Both the right and left pendulums were 57 cm long, with a 200 g metal ring attached at the bottom of each.

The movement trajectories of the pendulums were recorded using a Sonic 3-Space Digitizer (SAC Corporation, Stratford, CT). A sonic emitter attached to the end of each pendulum emitted sparks at the rate of 90 Hz. Microphones positioned in the four corners of the experimental enclosure registered the position of the emitters by computing the distance of the emitter from the three of four micro-

phones that recorded the least number of errors during the trial. This slant range time series was stored on an 80486-based microcomputer using MASS motion analysis software (ESI Technologies, Columbus, OH). MASS was then used to calculate the mean frequency of oscillation, primary angle of excursion, and ϕ. The primary measures of ϕ and SDϕ were then calculated for each individual trial. Since no order effects were found, all three measures were averaged across replications to obtain single data points for each experimental condition.

Procedure. Participants stood next to a wood-frame enclosure with forearm and wrist supports designed to allow for comfortable maintenance of the posture shown in Figure 1. Participants could swing each pendulum within the enclosure without any obstruction from the enclosure frame or from the other pendulum. Both wrists were aligned with the midline of the body and separated along the same line by approximately 10 cm. Subjects were instructed to create as smooth and as continuous a trajectory as possible, holding the pendulum firmly in the hand to guarantee rotation about the wrist rather than the finger joints. On any given trial, participants were instructed to coordinate the hand-held pendulums to establish either muscular in-phase ($\psi = 0$) or anti-phase ($\psi = \pi$) 1:1 frequency locking either with or without visual guidance. They were permitted to elect a comfortable frequency and to signal the experimenter when they felt prepared for data collection in each 45 s trial. All experimental procedures reported in the present experiments adhere to the ethical guidelines of the American Psychological Association.

Results and Discussion

Separate analyses of variance (ANOVA) were conducted on $\phi - \psi$ and SDϕ. $\phi - \psi$ was positive and statistically equal for both $\psi = 0$ (3.2° or 0.06 rad) and $\psi = \pi$ (2.5° or 0.04 rad), $F(1, 8) = 2.09$, $p > .05$. $\phi - \psi$ was similarly positive and statistically equal both with (2.3° or 0.04 rad) and without (3.2° or 0.06 rad) visual information, $F(1, 8) = 3.59$, $p > .05$. The $\psi \times$ Vision Condition interaction was nonsignificant, $F < 1$. Therefore, neither intended phase nor visual information influenced the location of the equilibria.

Intended phase did have a significant effect on equilibria stability, as measured by SDϕ. Specifically, muscular anti-phase was significantly more variable (SDϕ = 9.8° or 0.17 rad) than muscular in-phase (SDϕ = 6.5° or 0.11 rad), $F(1, 8) = 24.99$, $p < .001$. There was no effect of visual information (SDϕ = 8.5° or 0.15 rad when eyes were open; SDϕ = 7.95° or 0.14 rad when eyes were closed), $F(1, 8) = 1.08$, $p > .05$, nor was there an interaction between ψ and visual condition, $F(1, 8) = 1.83$, $p > .05$.

The nonsignificance of the main manipulations on $\phi - \psi$ was expected from the perspectives of both hypotheses. With respect to SDϕ, the visual dominance hypothesis predicted no main effect of ψ (the higher stability of in-phase with eyes closed would be offset by its lower stability with eyes open, with the reverse true for anti-phase) but an interaction of ψ and vision. In contrast, ψ was significant and there was no interaction. The visual modulation hypothesis fared no better. Its prediction was simply that SDϕ would be less when the eyes were open. To the contrary, SDϕ was indifferent to the availability of vision.

The present results are accommodated by Equation 1. When $\delta = 0$, the contributions of the two oscillators to the coordination dynamics are identical. For this symmetrical case, the dynamics expressed by Equation 1 are such that anti-phase

is less stable than in-phase, and parameter variations do not affect the location of the attractors, only their stability (for empirical verification see Schmidt et al., 1993; Sternad et al., 1992; Sternad, Amazeen, & Turvey, 1996; Treffner & Turvey, 1995). Consequently, a possible conclusion to be drawn from Experiment 1 is that the level of space, insofar as it is represented by the present visual manipulation, does not affect the level of synergies when the intersegmental rhythmic coordination dynamics are symmetrical. In Experiment 2 we examine the influence of vision when the symmetry of the coordination dynamics is broken, that is, $\delta \neq 0$ rad $\cdot$ s^{-1}.

Experiment 2

Figure 2 shows the predictions from Equation 3 for the visual-haptic (eyes open) and haptic-only (eyes closed) conditions when $\delta = 0$, $\delta = \pm 1$, and $\delta = \pm 2$ rad $\cdot$ s^{-1} ($a = b = 2$, $c = 1$). The expectations are that (a) in-phase and anti-phase coordination will be defined by muscular, not spatial, criteria in both the occluded and visible conditions; (b) the equilibria of the elementary synergy under broken symmetry ($\delta \neq 0$) will be tuned closer to the muscularly defined 0 and π by visual control; and (c) the equilibria will be rendered more stable by visual control.

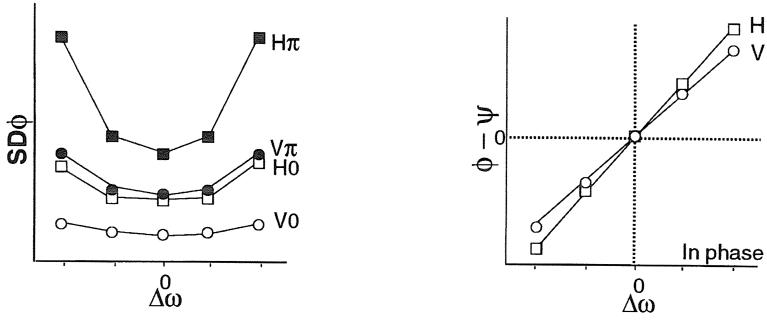

Figure 2 — Predictions from Equation 3 for haptic-only (eyes closed) and visual-haptic (eyes open) guided coordination as a function of detuning. Left panel: predictions for the standard deviation of relative phase (simply, the value of $1/|\lambda|$) in the visual-haptic (V) and haptic-only (H) conditions for both in-phase (0) and anti-phase (π) modes. Right panel: predictions for fixed-point shift for the haptic-only (H) and visual-haptic (V) conditions in the in-phase mode.

Method

Participants. Four men and 3 women, all graduate students at the University of Connecticut, participated on a voluntary basis. Five of the participants had participated previously in experiments using the hand-held pendulums procedure, but none had taken part in Experiment 1.

Design. A detuning factor with five levels ($\delta = 0, \pm 1, \pm 2$ rad $\cdot$ s^{-1}) was added to the design of Experiment 1, resulting in a three-way repeated-measures design with 20 conditions (2 ψ $\times$ 2 Vision Conditions $\times$ 5 δ) and only one trial per condition. Trials were 45 s each and order was completely randomized.

Apparatus and Data Collection. Detuning was manipulated through the addition of two asymmetrical pendulum pairs ($\delta = \pm 1, \pm 2$ rad $\cdot$ s^{-1}) to the one symmetrical pair ($\delta = 0$ rad $\cdot$ s^{-1}) used in Experiment 1. The unforced, undamped frequency of a hand-held pendulum was computed in the standard way (e.g., Amazeen, Schmidt, & Turvey, 1995; Sternad et al., 1992). We found that $\delta = \pm 1$ when a 44 cm pendulum with a 500 g metal ring (5.21 rad $\cdot$ s^{-1}) was paired with a 68 cm pendulum with a 200 g metal ring (4.20 rad $\cdot$ s^{-1}); $\delta = \pm 2$ when a 36 cm pendulum with a 90 g metal ring (6.28 rad $\cdot$ s^{-1}) was paired with a 66 cm pendulum with a 200 g metal ring (4.28 rad $\cdot$ s^{-1}). In either case, $\delta < 0$ when the longer (slower) pendulum was held in the left hand and $\delta > 0$ when the longer (slower) pendulum was held in the right hand. The coupled eigenfrequency of the pendulum pair was identical across all δ, $\omega = 4.60$ rad $\cdot$ s^{-1} (see Sternad et al., 1995; Treffner & Turvey, 1996). Data collection and experimental procedure for Experiment 2 were identical to Experiment 1.

Results and Discussion

Separate ANOVAs were conducted on $\phi - \psi$ and SDϕ. Variations in δ produced a significant shift of equilibria away from intended phase, $F(4, 24) = 63.649$, $p < .0001$. Note in Figure 3 that $\delta > 0$ produced $\phi - \psi > 0$, and $\delta < 0$ produced $\phi - \psi < 0$. There was no main effect of either ψ, $F < 1$, or vision condition, $F < 1$, on $\phi - \psi$. The expected interaction between vision and δ was significant, $F(4, 24) = 11.439$, $p < .0001$, as shown in Figure 3, with fixed-point shift amplified in the absence of vision. Figure 4 depicts the unexpected $\psi \times \delta$ interaction, $F(4, 24) = 11.890$, $p < .0001$: The fixed-point shift was larger when $\psi = 0$ than when $\psi = \pi$. The $\psi \times$ Vision Condition was nonsignificant, $F < 1$, but, as shown in Figure 5, there was a three-way interaction, $F(4, 24) = 4.218$, $p < .01$. The attenuation of fixed-point shift by visual information was more effective in the spatial in-phase (muscular anti-phase) condition than in the spatial anti-phase (muscular in-phase) condition.

Figure 6 depicts SDϕ as a function of ψ and δ. In replication of Experiment 1, muscular anti-phase (9.7° or 0.17 rad) was significantly more variable than muscular in-phase (8.4° or 0.14 rad), $F(1, 6) = 9.62$, $p < .05$. As expected, SDϕ increased with increasing $|\delta|$, $F(4, 24) = 51.47$, $p < .0001$. Visual information had no significant effect on variability, $F < 1$, nor were any of the interactions significant, $F < 1$.

Experiment 1 showed that vision did not affect the fixed point of symmetrical coordination dynamics, $\delta = 0$. This indifference to vision at $\delta = 0$ was corroborated in Experiment 2, as shown by Figure 3. However, vision did affect coordination equilibria, as expected, when $\delta \neq 0$. The shift in fixed point induced by breaking reflective symmetry was attenuated by the eyes-open condition. Also, as evidenced by the significant three-way interaction shown in Figure 5, attenuation of fixed-point drift by vision was greater in magnitude for the muscular anti-phase (spatial in-phase) condition than for the muscular in-phase (spatial anti-phase) condition. As should be obvious from Figure 1, the arrangement of the coordination in the frontoparallel plane makes the muscular in-phase (spatial anti-phase) condition harder to monitor visually by following the bottom of the pendulums (as subjects were instructed to do) than the muscular anti-phase (spatial in-phase) condition. This suggests why visual monitoring of the coordination was more effective for attenuating fixed-point drift in the spatial in-phase than in the spatial anti-phase condition.

Although vision influenced location of the equilibria, it did not influence their degree of stability as measured by SDϕ. The increase in variability accom-

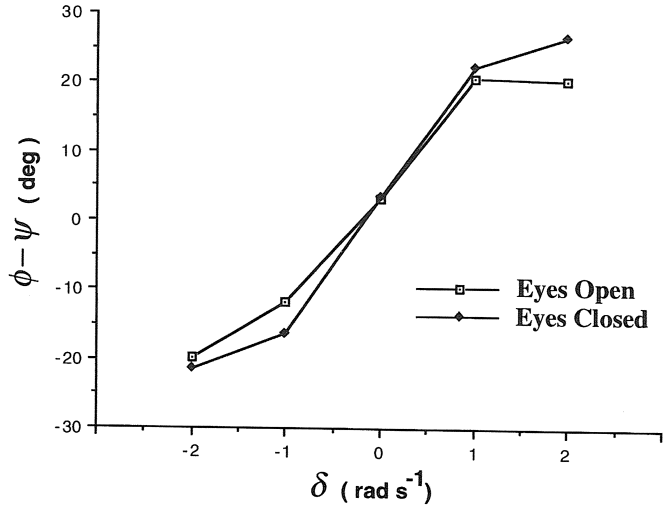

Figure 3 — Significant interaction of detuning and vision (eyes open vs. eyes closed) in Experiment 2 showing the attenuation of fixed-point shift in the eyes-open condition.

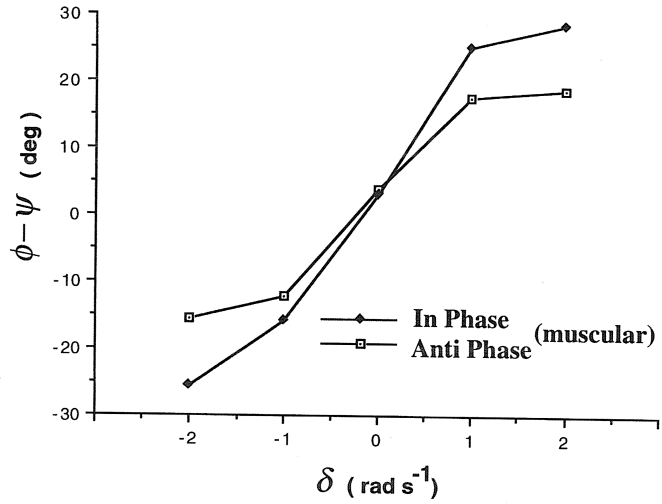

Figure 4 — Significant interaction of detuning and phase mode in Experiment 2. The muscular in-phase (spatial anti-phase) mode registered greater fixed-point shift due to detuning than the muscular anti-phase mode.

panying detuning from 0 and π was not smaller when the eyes were open than when the eyes were closed. Typically, for intersegmental coordination of movements parallel to the sagittal plane, larger fixed-point shifts are accompanied by larger SDϕ (Schmidt & Turvey, 1994; Schmidt et al., 1993; Sternad et al., 1996; Treffner & Turvey, 1995, 1996). The interpretation for this linkage is readily given

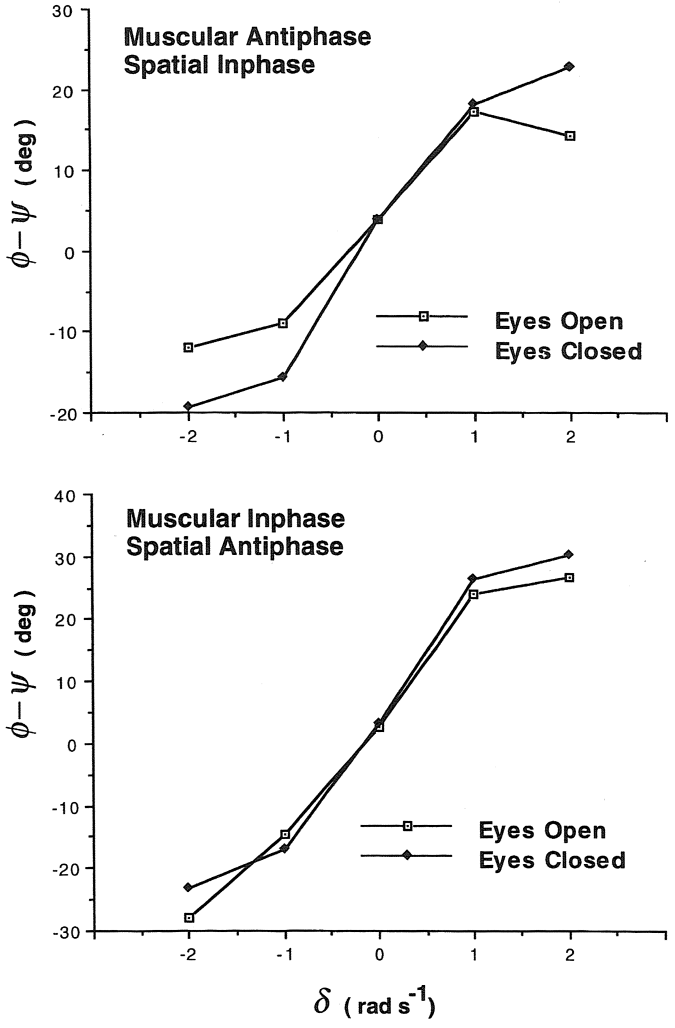

Figure 5 — Three-way interaction of detuning and vision in Experiment 2. Attenuation of fixed-point shift due to detuning was more pronounced in the muscular anti-phase (spatial in-phase) condition (top panel) than in the muscular in-phase (spatial anti-phase) condition (bottom panel).

in terms of the underlying potential function $V(\phi)$ from which Equation 1 is derived as $-d\ V(\phi)/d\phi$ (see Haken et al., 1985). As the minima of the potential function, that is, the attractors, are displaced from 0 and π, the potential wells around the minima become more shallow with the result that a stochastic force of strength Q can displace the system from the minima to a larger degree. Hence, SDϕ is systematically amplified with fixed-point shift. The present results suggest that for intersegmental coordination of movements parallel to the body's lateral plane, displacements of the minima of the potential function and the steepness of the poten-

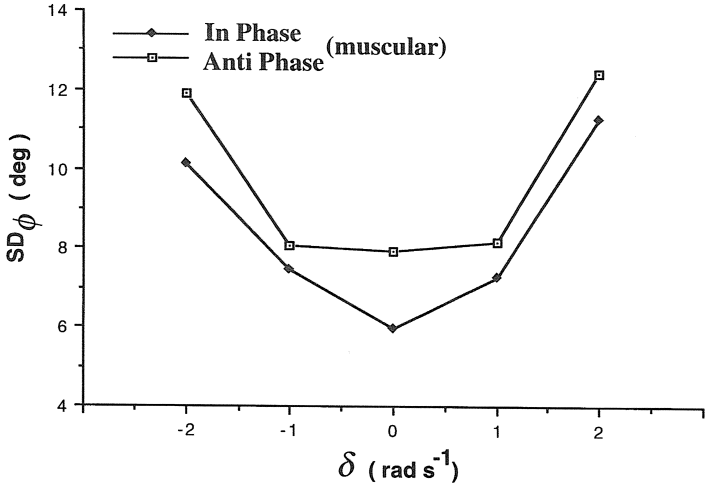

Figure 6 — Greater variability of muscular anti-phase shown over the entire detuning range used in Experiment 2.

tial walls surrounding the minima do not change together. There is the suggestion of a dissociation between fixed point and stability.

This preceding dissociation and the contrast between the intersegmental coordination investigated here and in prior experiments are underscored by the observation in Experiment 2 that muscular in-phase was more susceptible to symmetry breaking (detuning) than muscular anti-phase. Equations 1 and 3 predict the opposite, and previous investigations have confirmed this prediction (e.g., Amazeen, Sternad, & Turvey, 1996; Sternad et al., 1996; Treffner & Turvey, 1995, 1996). Importantly, the greater susceptibility of muscular in-phase to detuning was not accompanied by a reversal of stability as measured by SDϕ. By this measure, muscular in-phase was more stable than muscular anti-phase, in agreement with theory and experimentation. Patently, the anomolous nature of greater susceptibility of muscular in-phase to detuning calls for a systematic replication of this major observation of Experiment 2.

It is evident that vision did not dominate the coordination pattern in Experiment 2. If visual domination occurred with eyes open, then $\phi = 0$ and $\phi = \pi$ in muscular coordinates would have become $\phi = \pi$ and $\phi = 0$, respectively, in visual–spatial coordinates, and an interaction between vision and ψ would have been observed. Additionally, in the presence of vision, SDϕ should have been larger for $\phi = 0$ in muscular coordinates than $\phi = \pi$ in muscular coordinates. Neither of these effects, which were expected from the hypothesis of visual dominance, were confirmed. At the same time, it is clear that Equation 3 accommodates the present data only in part, and major expectations from Equation 3 were not upheld. In sum, the present experiment strongly hints that coordination dynamics for movements perpendicular to the body's sagittal plane, and the contribution of vision, may not conform to a straightforward extension of Equation 1.

Finally, the unexpected results raise the possibility that all or part of the anomaly in pattern arises due to peculiarities of the specific experimental arrange-

ment rather than more general properties of coordinations in the coronal plane. It is possible, for instance, that the apparatus and the subject's position in it constrained or otherwise altered the performance conditions that have provided the well-known results of coordination parallel to the sagittal plane. Ease of movement between the two arms may not have been balanced, or there may have been significant differences in amplitude of motion between arms or experimental conditions that might affect the interpretation of results. Also, it is possible that the present task induces a strategy for synchronization that is distinct from the one used by subjects in the standard version (oscillations parallel to the sagittal plane). It has been suggested that, in bimanual rhythmic coordination in general, the essential information for coordination is localized in discrete regions (or points) in relative phase space (Beek, 1989; Beek, Turvey, & Schmidt, 1992; Byblow, Carson, & Goodman, 1994; Kelso, 1995). These are possibilities that cannot be adequately addressed through the global measures employed in the present study but can be tested and eliminated only through extensive analysis of the measures of coordination at different phases of each cycle. Inspection of sample time series obtained in the present experiment does not, however, indicate any obvious peculiarities. Figures 7a and 7b present 10 s samples of a typical subject's time series in Experiment 2 as recorded from the bottom of each hand-held pendulum. Figure 7a presents in-phase and anti-phase (in spatial coordinates) data in the eyes-open and eyes-closed conditions for the symmetrical oscillator case ($\delta = 0$), and Figure 7b presents the same data for the most extreme asymmetry condition ($\delta = 2$) used in Experiment 2 (and in the following Experiment 3). No obvious anomalies are visible in either data set. In Figure 7b, showing $\delta = 2$, the asymmetry with the longer pendulum in the right hand is most likely responsible for the visible difference in position amplitude. Otherwise, the time series do not appear to contain anomalies of the kind just discussed.

Experiment 3

Experiment 2 was replicated with one important change. In Experiment 2, the movement frequency at which the two pendulums moved together was essentially constrained by the sizes of the pendulums. Participants selected a movement frequency that was comfortable for the given coupled-pendulum condition. When participants make these selections, the frequencies chosen tend to correlate with the natural frequencies of the pendulum pairs (computed as if the coupling between hand-held pendulums was rigid, e.g., Amazeen et al., 1996; Sternad et al., 1996), although different participants tend to select different frequencies. In Experiment 3, the movement frequency was dictated by metronome rather than selected freely. Variation in this aspect of the coordination dynamics was thereby eliminated. A possible drawback of using metronome control is that the explicit emphasis on controlling movements by hearing may diminish the implicitly defined contribution of vision (performing the coordination with eyes open versus eyes closed). Of major significance in Experiment 3 was whether muscular in-phase would be more susceptible to detuning with respect to fixed-point shift, but less destabilized by detuning as measured by $SD\phi$, than muscular anti-phase.

Method

Participants. Four men and 4 women, all graduate students at the University of Connecticut, participated on a voluntary basis. Four of the participants had

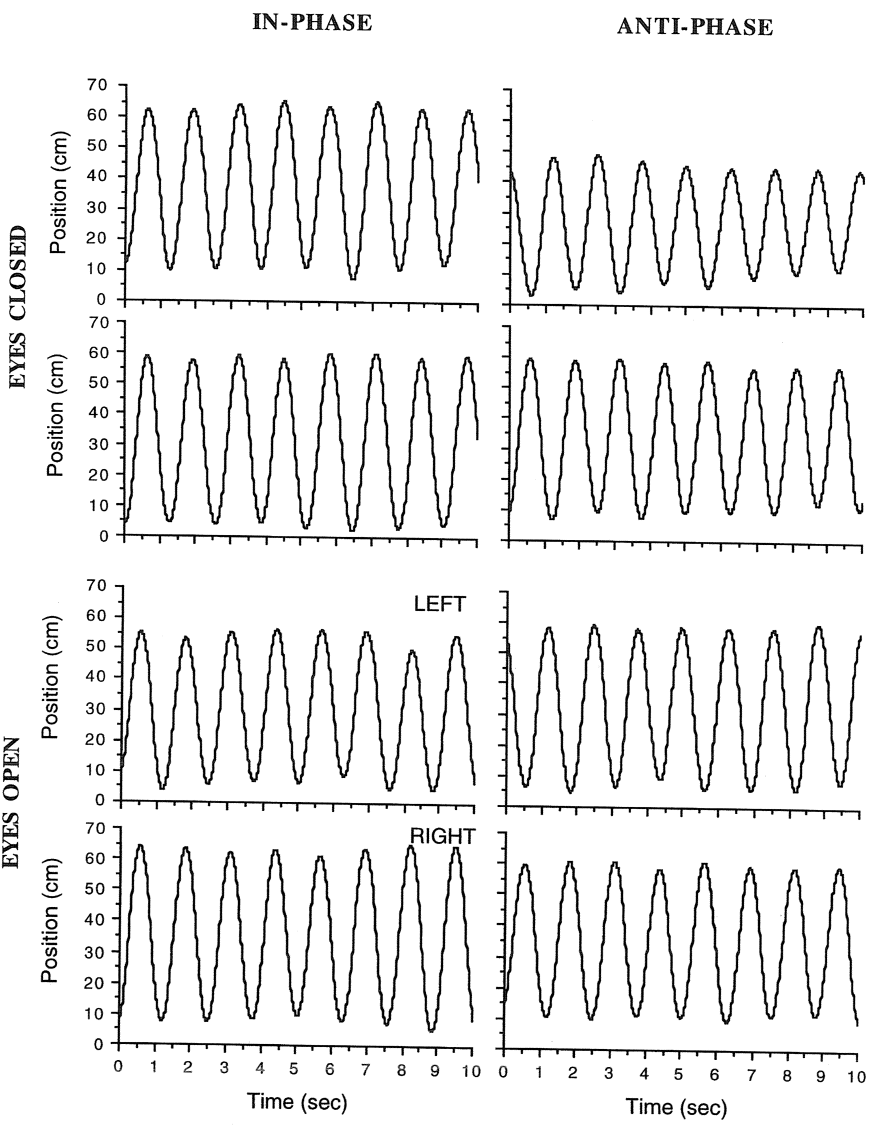

Figure 7 — Sample time series of pendulum positions during 10 s of data collection in Experiment 2 from a typical subject: (A) symmetrical pendulum condition, and (B) asymmetrical pendulum condition. In each case, pendulum positions were recorded from the bottom of each pendulum.

taken part previously in interlimb coordination experiments involving hand-held pendulums. None had participated in any of the preceding experiments of the present series.

Design. The same three-factor, repeated-measures design (2 ψ × 2 Vision Conditions × 5 δ) used in Experiment 2 was used in Experiment 3.

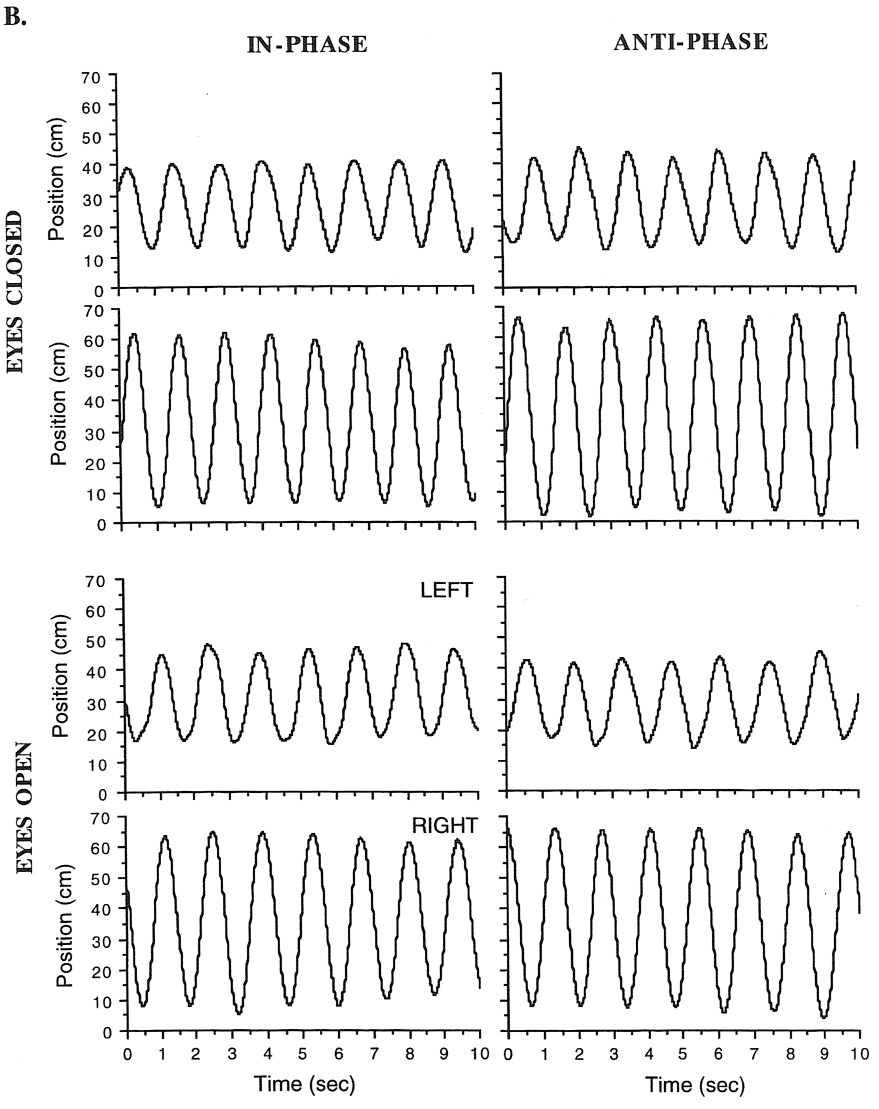

Figure 7 — ***(continued)***

Apparatus and Data Collection. Apparatus was identical to Experiment 2. Because $\omega = 4.60$ rad · s^{-1} for all three pendulum pairs, the same metronome frequency was used to pace participants in all three δ conditions. Otherwise, data collection was identical to Experiment 2.

Procedure. For each trial, participants were asked to produce the required in-phase or anti-phase coordination and to try at all times to keep pace with the metronome. Participants were advised, but not required, to try to synchronize with the metronome at times when one or both pendulums reached peak extension in the

cycle. Observation of performance suggested that participants found it convenient to follow the guideline. On a trial, data collection was started once the participant signaled that he or she was satisfied with the stability of the pattern and its synchrony with the metronome. The procedure was otherwise identical to Experiment 2.

Results and Discussion

Separate ANOVAs were conducted on $\phi - \psi$ and SDϕ. In replication of Experiment 2, variations in δ produced significant shifts of equilibria away from intended phase, $F(4, 28) = 141.19$, $p < .0001$, with $\delta > 0$ producing $\phi - \psi > 0$ and $\delta < 0$ producing $\phi - \psi < 0$. There was no main effect of either ψ, $F < 1$, or vision condition, $F < 1$, on $\phi - \psi$. The $\psi \times \delta$ interaction was also replicated, $F(4, 28) = 3.58$, $p < .02$, with a greater fixed-point shift for $\psi = 0$ than for $\psi = \pi$ (see Figure 8). Unlike Experiment 2, the Vision Condition $\times$ δ interaction was nonsignificant, $F(4, 28) = 1.54$, $p > .05$, suggesting that experimental control of coupled frequency negated the amplifying effect that absence of vision had on fixed-point shift. Vision did not interact with ψ, $F < 1$, nor was there a three-way interaction, $F < 1$.

In replication of Experiments 1 and 2, anti-phase (10.2° or 0.18 rad) was significantly more variable than in-phase (9.1° or 0.16 rad), $F(1, 7) = 6.07$, $p < .05$ (see Figure 9). There was also a significant effect of δ on SDϕ, $F(4, 28) = 19.90$, $p < .0001$, with SDϕ least at $\delta = 0$ and increasing symmetrically for $\delta = \pm 1$ and $\delta = \pm 2$. Visual information had no significant effect on variability, $F < 1$, nor were any of the interactions significant: $\psi \times$ Vision Condition, $F < 1$; Vision Condition $\times$ δ, $F(4, 28) = 2.50$, $p > .05$; $\psi \times \delta$, $F(4, 28) = 2.34$, $p > .05$; $\psi \times$ Vision Condition $\times$ δ, $F(4, 28) = 1.60$, $p > .05$.

The main outcomes of Experiment 3 in relation to those of Experiment 2 were (a) the complete absence of an effect of vision and (b) a replication of the

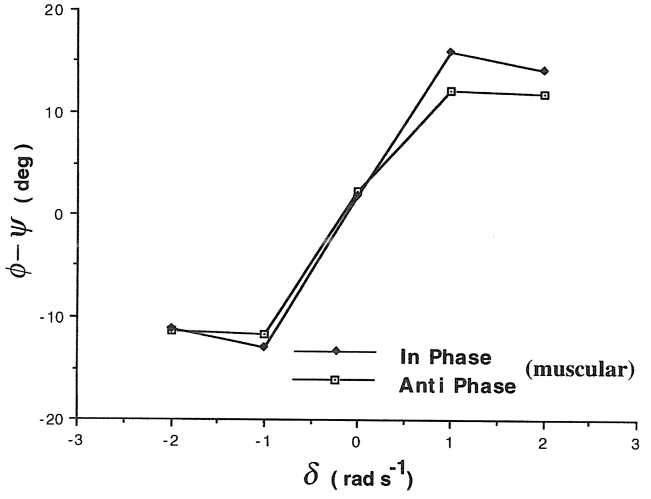

Figure 8 — Significant interaction of detuning and phase mode in Experiment 3. As in Experiment 2, muscular in-phase (spatial anti-phase) mode registered greater fixed-point shift due to detuning than the muscular anti-phase mode.

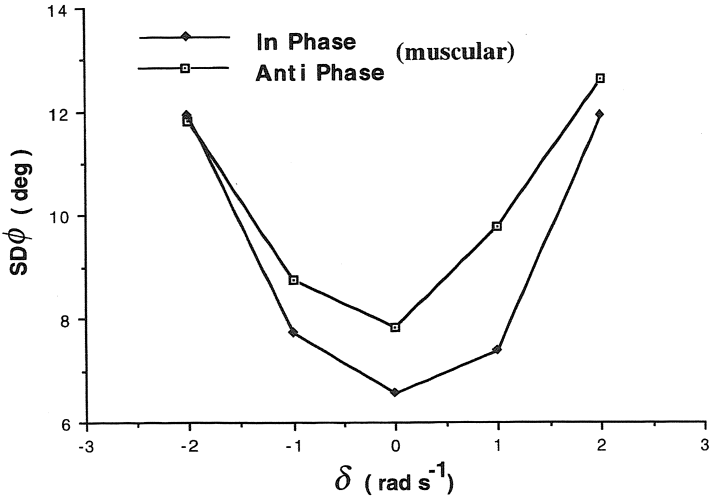

Figure 9 — Greater variability of muscular anti-phase shown over the detuning variation used in Experiment 3.

greater shift by symmetry breaking, but less destabilization by symmetry breaking, of equilibria under muscularly defined $\psi = 0$ than under muscularly defined $\psi = \pi$. The use of a metronome and the explicit requirement to track its frequency may have contributed to the elimination of the two-way interaction between vision and detuning and the three-way interaction between phase, vision, and detuning found in Experiment 2 and shown in Figures 3 and 5, respectively. If so, this would reinforce the impression that intersegmental rhythmic coordination is mainly through the haptic–proprioceptive perceptual system, that is, formed at Bernstein's level of synergies, with vision a potential but not automatic modifier of the resultant coordination dynamics.

The result expressed by (b) above is of major theoretical importance. The structure of Equations 1 and 3 cannot give rise to the observed opposition between fixed-point shift and variability. To be redundant, when the left-hand sides of these equations are set to zero and the equations solved to isolate the fixed points or zero crossings for given parameter values, and the slopes at these zero crossings are then determined (λ from Equation 2), it is necessarily the case that the larger the deviation of a zero crossing from 0 or π, the shallower is the corresponding slope. In short, the larger the fixed-point shift, the larger the variability (given that SDϕ is inversely related to λ). The question that the present anomalous finding poses is, Which measure, the magnitude of $\phi - \psi$ or the magnitude of SDϕ, most appropriately captures the difference between the two attractive states of $\phi \approx 0$ and $\phi \approx \pi$, given that the two measures behave differently? Experiment 4 addresses this question by examining phase transitions under scaling of movement frequency.

Experiment 4

In one of the earliest demonstrations of phase transitions in human intersegmental coordination, Kelso (1984) asked participants to oscillate their two index fingers

(or two hands) at a movement frequency specified by a metronome. With increasing movement frequency, the "prepared" anti-phase of a subject's fingers switched suddenly to in-phase. The direction of the transition (from anti-phase to in-phase) was not reversed by reducing the movement frequency, however, or by initially preparing the fingers in-phase. This observation of a greater persistence over frequency scaling of muscular in-phase coordination led to the 2π periodic function in Equation 1, which is the negative derivative with respect to ϕ of the potential function

$$V(\phi) = -a\cos - b\cos 2\phi. \quad (4)$$

The minimum of this function at $\phi = 0$ is greater than the minimum at $\phi = \pm\pi$. The ratio of the coefficients, *b/a*, defines a control parameter, as noted above, that is inversely related to the movement frequency. As *b/a* decreases, the potential wells become more shallow, with those at $\phi = \pm\pi$ disappearing when $b/a = 0.25$ (Haken et al., 1985). The spontaneous transition from anti-phase to in-phase, but not in reverse, is the consequence of the loss of stability (loss of the attractor) at $\phi = \pm\pi$ with increasing movement frequency.

The phase transition methodology can be used, therefore, to determine the relative strengths of the attractors in the rhythmic coordination of movements perpendicular to the sagittal plane. That is, it can be used to answer the question, Which is the most attractive coordination in the present experimental task, in-phase coordination defined in muscular coordinates or anti-phase coordination defined in muscular coordinates? In concrete terms, the test is whether the muscular in-phase mode will switch to the muscular anti-phase mode, and whether the muscular anti-phase mode will persist, with frequency scaling as implied by the fixed-point shift results of Experiments 2 and 3, or whether the reverse will be true as implied by the variability results of those experiments.

Method

Participants. Two women and 2 men, all undergraduates at the University of Connecticut, participated in Experiment 4. All 4 subjects were enrolled in an introductory psychology course and received course credit for their participation.

Design. Participants were instructed to maintain a relative phase of either $\psi = 0$ or $\psi = \pi$ with either symmetrical ($\delta = 0$ rad $\cdot$ s^{-1}) or asymmetrical ($\delta = 2$ rad $\cdot$ s^{-1}) pendulums. There were 3 trials in each of 4 conditions (2 $\psi \times$ 2 δ) for a total of 12 trials. Order was completely randomized.

Apparatus and Data Collection. The system of symmetrical pendulums ($\delta = 0$ rad $\cdot$ s^{-1}) was composed of two identical pendulums that were 52 cm long and had 90 g metal rings attached at the bottom. The system of asymmetrical pendulums ($\delta = 2$ rad $\cdot$ s^{-1}) was composed of one 38 cm pendulum and one 69 cm pendulum, each with a 30 g metal ring attached at the bottom. The coupled eigenfrequency for both pendulum pairs was identical, $\omega = 5.08$ rad $\cdot$ s^{-1}. An auditory metronome paced the coordination, starting at 5.08 rad $\cdot$ s^{-1} and increasing every 10 s by 1.26 rad $\cdot$ s^{-1} to a maximum frequency of 11.38 rad $\cdot$ s^{-1}. Trials were 60 s long, with six frequency plateaus. Data collection began after the first 10 s plateau and continued for 50 s through five more plateaus. Data collection was otherwise identical to Experiments 1–3.

Procedure. On any given trial, participants were instructed to coordinate either symmetrical ($\delta = 0$ rad $\cdot$ s^{-1}) or asymmetrical ($\delta = 2$ rad $\cdot$ s^{-1}) pendulums to

establish either in-phase ($\psi = 0$) or anti-phase ($\psi = \pi$) without visual guidance and at the frequency designated by the metronome. They were informed that frequency would increase during the course of the trial and that they should track it to the best of their ability. Participants were also instructed that if they felt that they were losing the phase relation with which they began the trial, they should maintain it as long as possible but should not prevent themselves from switching to a more comfortable pattern. They were further reminded to continue swinging the pendulums (no matter what the pattern) until the end of the trial. Visual gaze was focused on a target provided at eye height on the wall in front of the participant.

Results and Discussion

For the 4 participants, transitions from muscular anti-phase to muscular in-phase occurred on 15 out of 24 frequency scaling trials; there were no trials on which transitions occurred from muscular in-phase to muscular anti-phase. In short, the experiment replicated the fundamental observations (Kelso, 1984), captured in the dynamics of Equation 1, that the muscular in-phase pattern is the more attractive and that with frequency scaling the muscular anti-phase pattern is the first to lose stability.

An important methodological feature of the present experiment is that many informal efforts to obtain a phase transition in the coordination of hand-held pendulums have not been successful. Those previous efforts, however, were restricted to movements parallel to the sagittal plane. In the present research, the focus was upon movements perpendicular to the sagittal plane, and we observed spontaneous switches in coordination in this orientation (see discussion of Experiment 2 and General Discussion section for possible distinctions between movements parallel and perpendicular to the sagittal plane). The general significance of this finding is that the hand-held pendulums procedure can now be used to investigate the phase transition phenomenon under conditions of systematic symmetry breaking. A most important prediction of Equation 1 in this respect follows from the fact that the bifurcation for the broken symmetry condition $\delta = \pm 2$ is different from that of the symmetry condition $\delta = 0$: a saddle-node bifurcation versus a subcritical pitchfork bifurcation (Kelso, 1994; Turvey & Carello, 1996).

Figure 10 shows the evolution of these two types of bifurcation with decreasing *b/a*. The subcritical pitchfork bifurcation arises when the two repellers at $\phi = \pi/2$ and $\phi = 3\pi/2$ "collide" with the attractor at $\phi = \pi$. This collision changes the attractor at π to a repeller, leaving only the attractor at 0. The prediction in this case is that the transition from muscular anti-phase to muscular in-phase must be discontinuous (see discussions for the general case in Hillborn, 1991; Strogatz, 1994). In contrast, the saddle-node bifurcation arises from a collision between the repeller at $\pi/2$ and the attractor at π, with an initial coalescing of the unstable and stable states followed immediately by the annihilation of both. Importantly, however, there is a saddle-node remnant or ghost that can continue to attract (from one direction) and repel (in the opposite direction) (Strogatz, 1994). Relative phase can get trapped temporarily in the vicinity of this ghost point (Kelso & Ding, 1993). The prediction, therefore, with regard to the transition from muscular anti-phase to muscular in-phase when $\delta \neq 0$ is that it will be gradual rather than discontinuous. Figure 11 presents examples of the phase transition under $\delta = 0$ and $\delta = \pm 2$. The transition is abrupt in the former symmetrical case and prolonged in the latter asymmetrical case, in agreement with the contrast in bifurcation types. The obser-

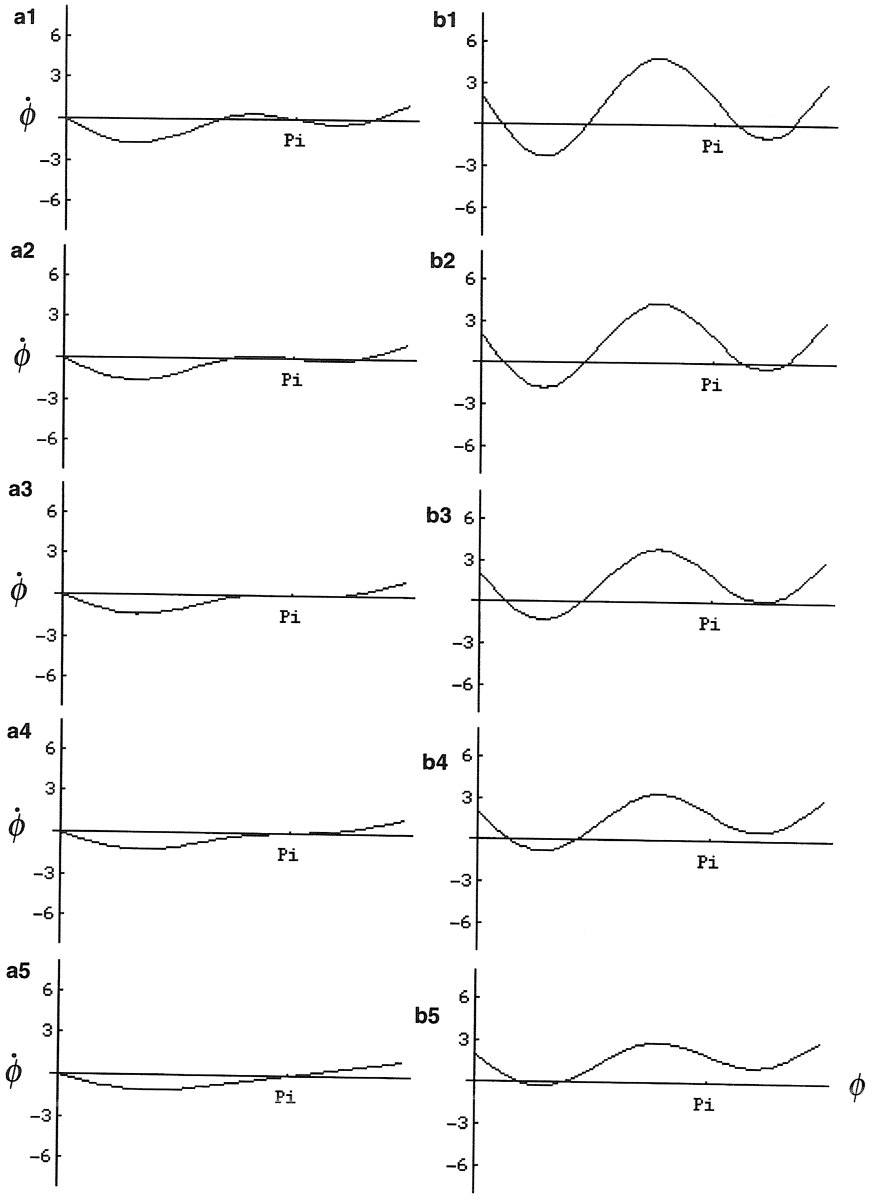

Figure 10 — Evolution of subcritical pitchfork (a1–a5) and saddle node or tangent (b1–b5) bifurcations with decreasing *b/a*. The subcritical pitchfork bifurcation changes the attractor at π to a repeller, leaving only the attractor at 0. The saddle-node bifurcation is an initial coalescing of the unstable and stable states followed immediately by the annihilation of both, leaving a saddle-node *ghost* that can continue to attract and repel.

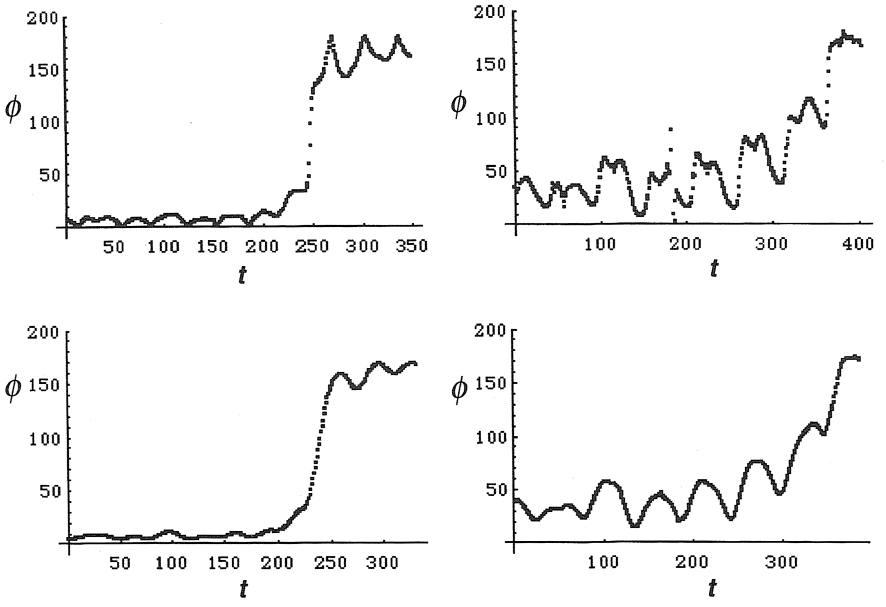

Figure 11 — Examples of the phase transition under $\delta = 0$ (left column) and $\delta = \pm 2$ (right column), with the lower panel in each column showing the smoothed data. The relative phase angles on the vertical axis are in spatial coordinates. The unit of time *(t)* on the horizontal axis is 1/90th of a second, the sampling rate used in the experiment. The series in the lower panel of both columns was obtained through an 18-point (0.2 s) moving average of the recorded data shown in the upper panels. The transition is abrupt in the former symmetrical case and prolonged in the asymmetrical case, in agreement with the contrast between subcritical pitchfork and saddle-node (or tangent) bifurcations.

vations reported in Figure 11 are of theoretical importance given their relation to intermittency phenomena (see discussions in Kelso, 1991, 1995; Kelso & DeGuzman, 1992). A future elaboration of the present experiment and analyses is planned.

General Discussion

The present series of experiments presents two important results with nontrivial implications for theories of intersegmental coordination dynamics. The first result is that visual guidance can attenuate the fixed-point shift associated with component asymmetries in interlimb 1:1 rhythmic coordination tasks, even as it produces no detectable changes in stability of the in-phase and anti-phase coordination modes. The second important result is that rotating the plane of motion of a basic bimanual coordination from the sagittal to the coronal plane can render the (muscular) in-phase mode more susceptible to fixed-point shift than the (muscular) anti-phase mode, even as the former mode remains more stable than the latter. As previously remarked, both of these results reflect a rather fundamental dissocia-

tion between fixed points and stability that is accommodated neither by Equation 1 nor by any parametric or expansional variations of it. Under these circumstances, one obvious possibility for a resolution appears to lie in the conventions used to define the collective variable of relative phase. The experiments reported here were directed at contrasting a neuromuscular convention based upon the homology of the involved muscle groups with a geometric convention based upon symmetries about either principal body axis. It is clear that a definition of relative phase based on neither convention renders the obtained results concordant with all predictions from Equation 1 or Equation 3.

At first sight, this outcome appears dissonant with several suggestions in the literature that the stability ranking of the two attractors (in-phase and anti-phase) in interlimb coordination dynamics is best characterized spatially rather than in terms of any preferred coupling among muscle groups (Baldisserra, Cavallari, & Civaschi, 1982; Baldisserra, Cavallari, Marini, & Tassone, 1991; Carson, Goodman, Kelso, & Elliot, 1995; Jeka & Kelso, 1995; Kelso, Buchanan, & Wallace, 1991; Kelso & Jeka, 1992;). Evidence for favoring the spatial characterization derives from empirical results obtained in coordination tasks involving rotations about the elbow and wrist joints (Kelso et al., 1991), the wrist and ankle joints (Baldisserra et al., 1982, 1991; Carson et al., 1995), and the elbow and knee joints (Kelso & Jeka, 1992). Results indicate that the coordination mode in which the participating limbs move in the same direction is more stable than the mode in which the limbs move in opposite directions. Moreover, for cases involving motions about the wrist joint, it has been shown that shifting from supinated forearm preparation to pronated forearm preparation (which reverses the mapping between wrist flexion–extension and direction of hand motion) does not alter the stability ranking of the spatially defined in-phase and anti-phase modes.

While these results highlight the limitations of defining relative phase strictly on the basis of muscle homology, a closer inspection of the above-cited studies reveals that they do not make a similarly convincing case for the considerably stronger claim that "the mutual direction of motion between interacting components and not simply kinesiological action of the participating muscles plays a role in determining coordinative stability" (Kelso & Jeka, 1992, p. 647). First, it is relatively easy to provide a perfectly satisfactory definition of relative phase based precisely on the "kinesiological action of the participating muscles" that gives results identical to those arrived at via spatial criteria in each of these studies. Second, it is equally easy to provide an obvious example, other than the present paradigm, of a coordination in which limbs moving in opposite directions produce a more stable pattern than limbs moving in the same direction.

Pursuing the former point first, we might observe that in all coordination patterns employed in the paradigms in question (i.e., wrist–elbow, wrist–ankle, and elbow–knee), a full oscillation of a given limb about a joint divides roughly into a half-cycle during which the rotation of the joint lifts the limb away from the ground plane (i.e., moves the limb against gravity) and a half-cycle during which the opposite rotation of the same joint lowers the limb toward the ground plane (i.e., moves the limb with gravity). In the case of a supinated arm, for example, wrist flexion elicits the lifting half-cycle and wrist extension elicits the lowering half-cycle, while for a pronated arm, wrist extension elicits the lifting half-cycle and wrist flexion elicits the lowering half-cycle. Similarly, for arm motions about the elbow joint, elbow flexion elicits the lifting half-cycle, while for foot motions

about the ankle joint, dorsiflexion elicits the lifting half-cycle. While different limbs in different orientations recruit different muscle groups to perform the lifting and lowering half-cycles (Bernstein, 1967), it is clear that no matter what muscle group is actually doing the work, the lifting half-cycle requires greater effort than the lowering half-cycle.

This fact of differential loading during the two half-cycles about any of the three joints can be used to define relative phase based purely on criteria involving the kinesiological action of the muscle groups involved in an interlimb (or intersegment) coordination task. We might define in-phase coordination as the organization in which both limbs (segments) traverse their lifting half-cycles together, and anti-phase coordination as the organization in which one limb (segment) traverses its lifting half-cycle while the other traverses its lowering half-cycle. These definitions of in-phase and anti-phase modes are based upon criteria of equal or unequal muscular effort required for concurrent movement of participating limbs (segments). We might predict, then, that the in-phase mode will be more stable than the anti-phase mode and conjecture that this is so because the simultaneity of the lowering half-cycles in this mode allows more time between lifting activity (summed over all involved muscles), rendering the mode energetically (or even informationally) more and more economical (compared to anti-phase) as the frequency of oscillation increases. While the conjecture may or may not be correct, the above definitions of in-phase and anti-phase capture every piece of data from each study under scrutiny. In-phase, by this definition, is always more stable than anti-phase, even though the definitions were arrived at through kinesiological criteria.

It remains true, however, that the kinesiologically based phasing convention developed above gives the same phase modes as the spatial criterion that takes movement of component limbs (segments) in the same direction as in-phase and movement in the opposite direction as anti-phase. As such, these two conventions are behaviorally indistinguishable for all of the tasks under consideration, and the obvious and relatively uninteresting reason for this is that gravity always acts in the direction of the ground plane. This brings us, however, to our second point, that it is possible to provide an example of an interlimb (segment) coordination, other than the one presented in this series of experiments, in which limbs moving in opposite directions produce a more stable coordination than limbs moving together in the same direction. Consider, then, the finger-oscillation task (Kelso, 1984) with an important twist: One arm is prepared supinated while the other is prepared pronated. By trying to oscillate their two index fingers with their arms held in the prepared orientations, readers can see that the spatially anti-phase mode (i.e., one finger rotates downward as the other rotates upward) is far more stable than the spatially in-phase mode. While gravitational loading on a finger is minimal due to its low mass, there remains an asymmetry in required muscular effort between flexing the finger away from the palmar plane and extending the finger toward this plane. Thus, while the spatial criterion fails to predict stability ranking, the kinesiological criterion developed above is still able to predict that the in-phase mode is more stable than the anti-phase mode.

Having thus reinforced the need to retain some suitable form of kinesiological criteria for phase mode identification, we may return to the rotated hand-held pendulums paradigm employed in the present study and note first that this paradigm introduces a dissociation between a spatial and any possible kinesiological definition of phasing in a manner that the wrist–elbow, wrist–ankle, or elbow–

knee paradigms do not. Applying the kinesiological criterion introduced above, we are able to predict the stability ranking of the two modes but are unable to reconcile that prediction with the pattern of fixed-point shift. On the other hand, adopting the spatial criterion applied in the studies cited above, we are able to predict the pattern of fixed-point shift (i.e., spatial in-phase produces smaller fixed-point shift) but are unable to reconcile that with stability ranking. In light of this quandary, we try in the following to take a fresh look at interlimb coordination by situating the dynamics of articular synergies, and indeed the interpretation of our variables of measurement, in a somewhat broader context of general theories of complexity.

In differentiating levels of motor coordinative organization in biological systems, Bernstein conceived of the level of muscular–articular links (his Level B) as concerned exclusively with formation and retention of stable patterns involving large numbers of disparate musculoskeletal components. The synergies assembled by this level of organization in the execution of intended tasks are deployed by the level of space (Bernstein's Level C), which may orient or adapt the coordination to the specific spatial contingencies of the task in question. The elegance of this level-encapsulated design is that two staggeringly complex responsibilities—harmonizing the activity of the various participating articulators into a stable and repeatable pattern (synergy), and channeling the synergy along a given perceptually determined trajectory—are relegated to two quasi-autonomous functional organizations. A perception–action complex composed of such Bernsteinian subsystems is close in spirit to the nearly decomposable architecture of complexity (Simon, 1962; Simon & Ando, 1961), which is characterized by the following two properties: (a) The short-term behavior of each component organization is approximately independent of the short-term behavior of the other component organizations, and (b) the long-term behavior of any one of the component organizations depends only in an aggregate manner on the behavior of the other components, that is, on the sum of their respective states averaged over time (see Simon, 1962, for further details).

The nearly decomposable architecture is ubiquitous in the natural world and has been identified as being operational at scales ranging from the economic and political (Fisher, 1961; Fisher & Ando, 1962) down to the atomic and molecular (de Groot, 1951). In considerations of the vibratory behavior of microphysical complexes, for example, the vibrations associated with nuclear processes are of higher frequency than those associated with the planetary electrons, which, in turn, are of much higher frequency than those associated with molecules. With respect to a dependent measure such as radiation frequency, then, a molecular organization is a nearly decomposable one: the short-term (high-frequency) behavior of molecular radiation relates to the short-term behaviors of the component atomic and subatomic organizations, and the long-term (low-frequency) aggregate radiation behavior relates to the interactions between those component organizations.

In studying a perception–action complex such as the one that accomplishes intersegmental 1:1 rhythmic coordination, interest is commonly focused on the behavior of two dependent measures: (a) the relative phase, whose distribution points to the regions of stability in phase-space (or the locations of the wells of the governing potential), and (b) the standard deviation of relative phase, which reflects stability magnitudes (or the steepness of the potential wells). If Bernstein's Levels B and C are viewed to couple in nearly decomposable fashion, critical insights become available in interpreting and predicting the two dependent measures under changing conditions at both Levels B and C. The first suggestion is

that the fixed-point behavior of the coordination (or the average relative phase) is a long-term, aggregate measure reflecting the interactions between Level B, which assembles and maintains the fundamental synergy, and Level C, which employs perceptual information (haptic, visual, and auditory) in orientating or adapting the coordination to the intended spatial configuration. The second suggestion is that the standard deviation of relative phase is a measure of the level of short-term, high-frequency behavior due primarily, if not completely, to processes and interactions occurring within Level B.

Several predictions follow from the above mapping of experimental measures to nearly decomposable Level B–Level C coupling. The first prediction is that the standard deviation of relative phase will reflect the exigencies of multicomponent pattern assembly and harmony retention that are peculiar to Level B. The behavior of this measure will be closely tied to the kinesiological demands operating upon assembled muscle groups and other biomechanical and physiological contingencies of synergy formation, and will retain some signature of Level B contingencies across changes in Level C configurations. The second prediction is that standard deviation of relative phase will scarcely, if ever, register qualitative changes as a function of changes in Level C contingencies. And the third prediction is that although fixed-point behavior, an interaction variable, will exhibit sensitivity to changes in Level B dynamics, it will also reflect changes in Level C contingencies.

These three predictions, which follow directly from conceptualizing Level B–Level C complex as a nearly decomposable system, account for every effect recorded in the series of experiments reported here. With respect to the first prediction, we may note that in Experiments 1 through 3, standard deviation of relative phase uniformly showed that the muscularly anti-phase coordination (which was prepared so as to be spatially in-phase) was less stable than the muscularly in-phase coordination (which was prepared so as to be spatially anti-phase). Moreover, Experiment 4 demonstrated that scaling the frequency of the coordination resulted in the loss of stability of the muscular anti-phase mode, resulting either in abrupt phase transitions to the muscular in-phase mode (when the interlimb system was symmetrical) or in excessive phase wandering (when the symmetry of the interlimb system was broken). Thus, the assembly of the synergy (by Level B) out of muscle groups producing synchronous lifting half-cycles (in-phase) or asynchronous lifting half-cycles (anti-phase) captures the pattern of standard deviation results. Along the same lines, with respect to the second prediction, it is worth noting that in Experiment 2, where the availability of visual guidance attenuated fixed-point shift due to detuning, no effects of vision were recorded on the standard deviation of relative phase. The availability or usability of visual information, and its effects on the observed coordination, are contributions from Level C contingencies. If, as postulated, standard deviation of relative phase reflects Level B–intrinsic behavior, the absence of any vision effects is clearly expected.

That leaves the third prediction, which speaks directly to the result in Experiments 2 and 3 that appears discordant with Equation 1 and Equation 2, namely, that the muscular in-phase coordination, traditionally known to be more stable than muscular anti-phase (and corroborated to be so throughout the present study), showed greater fixed-point shift due to detuning than did the muscularly anti-phase coordination. This result is unobtainable through Equation 1, Equation 3, or, for that matter, any equation that models the stability of a coordination as being purely derivative of its relative phasing behavior. The present paradigm differs from the

standard hand-held pendulums paradigm (Kugler & Turvey, 1987) solely in that the coordination is parallel to the coronal plane as opposed to parallel to the sagittal plane. The standard paradigm has been used to thoroughly explore and confirm the entire range of predictions made by Equation 1 and its variants (see Schmidt & Turvey, 1995, for a summary). The inability of this class of equations to accommodate the reported reversal of the fixed-point shift effect suggests that the present paradigm exposes previously unexplored levels of organization whose influences cannot be subsumed under the current quantitative understanding of intersegmental coordination dynamics. More specifically, the accepted generality of Equation 1 stems precisely from the conflation of Bernstein's level of synergies and his level of space in the standard paradigms. In both the standard hand-held pendulums and the finger-oscillation paradigms, the muscular definition of phase is completely interchangeable with the spatial definition of phase, leaving no opportunity to even discover if the distinction between the two conventions could have significance. The present research suggests that the pattern of fixed-point shift can be decoupled from that of coordination stability simply by eliminating the interchangeability of the muscular and spatial conventions.

In terms of the nearly decomposable Level B–Level C coupling model hypothesized here, the reversal of the fixed-point shift effect in Experiments 2 and 3 is not quite as perplexing if pictured as the signature of changes in Level C contingencies as we go from the standard to the current paradigm. Recall that in this view, aggregate relative phase behavior is considered an interaction variable that will show sensitivity to both Level B dynamics and Level C contingencies. Note first that changes in the level of detuning (Level B) *do* affect the interaction variable in that they produce fixed-point shift. But also, changes in Level C requirements (i.e., from orienting the synergy parallel to the sagittal plane in the standard paradigm, to orienting it parallel to the coronal plane in the current one) reverse the magnitude of shift. The standard quantitative model depicted in Equation 1 appears in this light as a special case solution that works when the Level C contingencies align perfectly with the inherent asymmetries of Level B dynamics, thereby allowing the modeling of $SD\phi$ (Level B variable) as a derivative of ϕ (Level B–Level C interaction variable). It is not surprising that changes in Level C requirements which add aspects to the behavior of the interaction variable independently of Level B dynamics are beyond the scope of the current model.

Aside from rendering potentially perplexing results at least marginally comprehensible, the method of nearly decomposable systems has the additional advantage of being recursively applicable over several levels of coordination structures. Consider, for example, the structure of the relatively well-studied case of Level B. Even as a study seeking to explore Level B–Level C coupling treats Level B as a relatively encapsulated subsystem, the internal complexity of Level B can itself be studied as a nearly decomposable system (see Turvey & Carello, 1996). The phase of each oscillator is influenced by the summed, aggregate effect of the relatively slowly changing spatiotemporal relations between the other oscillators in the coordination. At the same time, it exhibits little sensitivity to the fast-changing phase perturbations introduced into the other limbs' phasings by their own internal microstructural interactions. In fact, the key principles of nearly decomposable systems dovetail quite well with the central tenets of synergetics, and given the considerable success of the synergetic approach in illuminating the organization of Bernstein's Level B, it seems highly likely that

extending the study of interlimb coordination to issues of Level B–Level C coupling, and doing so in terms of intuitions from the theory of nearly decomposable systems, will benefit development of synergetic approaches that address phenomena at this level.

A final point that deserves mention has to do with the as-yet unfamiliar characteristics of Bernstein's Level C. The interface between fundamental coordination structures and information systems that modulate their deployment is undoubtedly one of the most majestic achievements of biological evolution. As such, the interactive influence of Level C as well as its internal structure and asymmetries will present daunting challenges for systematic exploration. Some hints of Level C asymmetries have peeped through even in the present study. Consider the fact that the fixed-point shift reversal effect of Experiment 2 was replicated with the introduction of the metronome in Experiment 3, but the visual attenuation of fixed-point shift disappeared under metronome-driven conditions. If both visual attenuation and configurational reversal of fixed-point shift are Level C contributions to Level B–Level C coupling, they clearly differ in their resilience against changes in Level B conditions. Tightening Level B coordination by a driver wiped out the effect of visual information on the interaction variable but did not alter the influence of spatial configuration. While it is clear that visual information can spatially constrain or modulate such a fundamental synergy as 1:1 interlimb coupling, it also seems interesting that its influence on highly fluid, well-practiced coordinations, when existent, comes only in the absence of, or perhaps at the expense of, precision timing performance. This would come as no surprise to players of racquet sports who have tried to correct a swing or impact angle by watching themselves strike the ball.

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Authors' Notes

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